Wilson Bull., 103(3), 1991, pp. 446–457

FOREST HABITAT LOSS, FRAGMENTATION, AND RED-COCKADED WOODPECKER POPULATIONS

RICHARD N. CONNER AND D. CRAIG RUDOLPH[1]

ABSTRACT.—Loss of mature forest habitat was measured around Red-cockaded Woodpecker (*Picoides borealis*) cavity tree clusters (colonies) in three National Forests in eastern Texas. Forest removal results in a loss of foraging habitat and causes habitat fragmentation of the remaining mature forest. Habitat loss was negatively associated with woodpecker group size in small populations that had relatively isolated clusters but not in a larger, more dense population. Cutting patterns also may affect the amount of foraging habitat available to a family group if the group is forced to go through the territories of other groups to access suitable foraging habitat. Habitat loss may affect woodpecker group size by causing an insufficiency of foraging habitat and dispersal-demographic problems. *Received 15 Jan. 1991, accepted 15 April 1991.*

Forest loss and fragmentation and its effects on wildlife have become an increasing concern of scientists, managers, and environmental groups over the past several decades (Harris 1984, Wilcove 1989). Historically, the effects of fragmentation are best known from theory and studies of insular biology (Preston 1962a, b; MacArthur and Wilson 1967). These and subsequent studies (Diamond 1973, 1976) examined the effects of island size and isolation on species richness and extinction rates. This concept was extended to the sizes of habitat fragments necessary to maintain species in preserves and woodland fragments (Diamond and May 1976, Galli et al. 1976, Wilcox 1980, Rosenberg and Raphael 1986).

In addition to problems created by size of forest fragments (Robbins et al. 1989) and dispersal distances between patches, fragmentation within a species home range may have detrimental effects other than simple loss of usable habitat. In mature forest species with large home ranges, dispersing young may have greater difficulty in finding a mate if numerous or extensive patches of nonforest exist within the general forest landscape. Two species that may suffer from this problem are the Spotted Owl (*Strix occidentalis*) and the Red-cockaded Woodpecker (*Picoides borealis*). Both species often have low-density populations with relatively isolated breeding units (Forsman et al. 1984, Ligon et al. 1986, Conner and Rudolph 1989). Habitat patchiness and fragmentation have been predicted to cause dispersal problems within forest habitat in Spotted Owls and other rare species (Lande 1988, Simberloff 1988, Doak 1989).

[1] Wildlife Habitat and Silviculture Laboratory (maintained in cooperation with the School of Forestry, Stephen F. Austin State Univ.), Southern Forest Experiment Station, USDA Forest Service, Nacogdoches, Texas 75962.

Conner and Rudolph (1989) made a preliminary investigation into the effects of forest loss, isolation, and fragmentation on group size in Red-cockaded Woodpeckers while studying population declines in Texas. Analyses indicated that woodpecker group size decreased as forest removal within a 400-m radius of active clusters (colonies, see Walters et al. 1988) increased. Although a group size decline could be caused by a reduction in foraging habitat, foraging areas available in the study were well above minimum requirements described in the recovery plan (USFWS 1985).

In this study, we evaluate relationships between Red-cockaded Woodpecker group size and measures of forest habitat loss and fragmentation in three National Forests in eastern Texas. Our study focuses on populations that are small, have relatively isolated family groups, and occupy a range of nonfragmented to highly fragmented habitat. These small populations are compared to a larger, more dense population. We examine and test the effects of forest loss (foraging habitat insufficiency) and forest fragmentation on Red-cockaded Woodpecker family group size. If group size is related to habitat loss, what is the cause of this relationship? Several hypotheses were formulated to explore this question: (1) If fragmentation is affecting female dispersal for mate replacement, habitat fragmentation around single male clusters should be greater than fragmentation around clusters with only breeding pairs; (2) If habitat loss (foraging insufficiency) is affecting woodpecker group size, habitat loss around clusters with only breeding pairs should be greater than habitat loss around clusters with breeding pairs and helpers. As an additional test to evaluate the effects of fragmentation vs foraging insufficiency on family group size, we compared small and large populations; (3) If habitat loss is affecting foraging sufficiency and fragmentation is not affecting dispersal, woodpecker group size should be a function of habitat loss in both large and small populations.

METHODS

We studied Red-cockaded Woodpeckers in the Angelina (ANF), Davy Crockett (DCNF), and Sam Houston (SHNF) National Forests in eastern Texas. Red-cockaded Woodpeckers on the ANF (62,423 ha) are found primarily in longleaf pine (*Pinus palustris*) habitat (14 active clusters) on the southern portion of the forest, while eight additional clusters are in loblolly (*P. taeda*)—shortleaf (*P. echinata*) pine habitat on the northern portion of the ANF. The northern eight active clusters are isolated from the other active clusters by a distance of more than 34 km and the 4+ km wide Sam Rayburn Reservoir. The DCNF (63,923 ha) is 32 km west of the ANF and primarily loblolly and shortleaf pine forest. Less than 1% of the DCNF is primarily longleaf pine. Active Red-cockaded Woodpecker clusters are primarily located in the northern half of the forest with two active clusters relatively isolated (26 km distant) in the southern extreme of the forest. The SHNF (65,218 ha) is about 30

km south of DCNF. Loblolly pine is the predominant pine species, although shortleaf pine is present in most stands and predominates on the drier sites. The 24 active Red-cockaded Woodpecker clusters in the eastern portion of the SHNF (San Jacinto Ranger District) are sparsely distributed with greater distances between clusters than in the western portion of the forest. The Raven Ranger District has a relatively large population of Red-cockaded Woodpeckers with more than 114 active clusters in the western portion of the SHNF. About 90 active clusters constitute a dense population in a portion of the Raven Ranger District where there is one active cluster per 389 ha of total forest area. Sparse populations in the rest of the SHNF and the ANF and DCNF average one active cluster per 2300 ha of total forest area.

Dawn and dusk visits were made to all known active clusters in the ANF and DCNF between March–June 1987 and late December 1987--June 1988 in the SHNF to determine the number of woodpeckers in each woodpecker family group. Ideally, group size in the SHNF should have also been measured during March and June when group size is lowest. A longer field season was necessary because of the large population size in the SHNF. Also, most mortality of young occurs during the first several months post fledging. If any bias is present, it should be distributed throughout the SHNF and not influence mathematical relationships. Location of each active and inactive cluster was determined on aerial photographs taken November–December 1986. Circles of 400 m and 800 m radii were drawn around clusters on xerographic copies of the aerial photographs (3.2 cm/km). A 400 m radius normally will include all cavity trees within a cluster, and an 800 m radius normally will include all foraging habitat used by a family group (USFWS 1985). All nonforest habitat (forest removal) including permanent private openings and lakes, clearcut stands, southern pine beetle treatment cuts, and pine plantations less than 20 years old >1.5 ha in area (see Conner and Rudolph 1989) were delineated within these two radii, cut out, and measured on a digital electronic area meter (to nearest 0.01 cm^2). Seed-tree and shelterwood regeneration areas where residual pines were still present were considered to be forest habitat because of the Red-cockaded Woodpecker's use of open pine savanna habitat (Patterson and Robertson 1981) and their frequent use of seed-tree and shelterwood areas (Conner et al. 1991). The number of separate cuts within the 400 and 800 m radii of each cluster was also counted. As an additional measure of habitat loss, an angular measure of nonmature forest habitat as viewed from the cluster center out to 800 m was summed (Fig. 1). Thus, if a cut was close to a cluster center, a larger angle would be required to view the lateral edges of the cut than for a similar cut that was farther away. Of these variables, the angular sum of nonmature habitat and the number of cuts may be better measures of fragmentation, whereas the percent of forest removal may be a better measure of habitat loss. Clearly, it is difficult to separate these two landscape characteristics. Also, the number of active clusters within 2 km of each cluster was also determined as a measure of isolation.

Active woodpecker clusters were initially divided into small ($\leq$two woodpeckers) and large ($>$two woodpeckers) family groups to test for relationships of group size with habitat loss. Variables measuring habitat loss and isolation were compared between large and small groups with *t*-tests. Separate variance estimates were used if variances between analysis groups were significantly different (SPSSX 1986). Spearman rank correlation was used to examine relationships between actual woodpecker group size and habitat variables. Logistic regression was used to determine if group size (small vs large) and cluster status (active and inactive) in small Red-cockaded Woodpecker populations were a function of habitat loss (Dixon et al. 1985).

Active clusters were then divided into three groups (single males, breeding pairs, and breeding pairs plus helpers) and compared to determine the relative contribution of fragmentation vs habitat loss to woodpecker group size. Habitat around single male clusters in

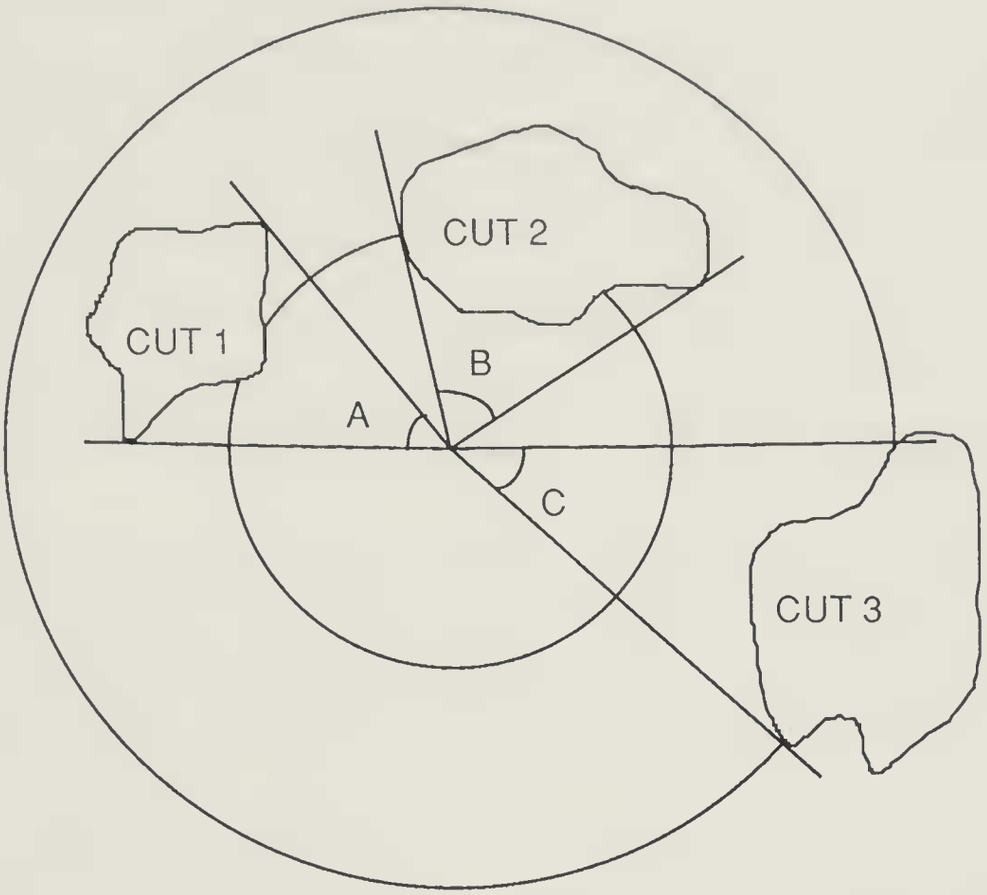

FIG. 1. Method used to measure the angular sum (ANGSUM) of nonforest habitat (cut areas) around active Red-cockaded Woodpecker clusters in eastern Texas. The sum of angles A, B, and C would yield the measurements for this particular cluster that would be at the center of the circles. The inside circle's radius is 400 m and the outside circle's radius in 800 m.

small populations was compared to habitat around clusters with only breeding pairs to determine if the ability of dispersing young female Red-cockaded Woodpeckers is hampered by habitat fragmentation. Habitat around clusters with breeding pairs was compared with habitat around clusters with pairs and helpers to determine if habitat loss affects the ability of an area to support woodpeckers. Habitat around clusters with only breeding pairs was compared to habitat around clusters with breeding pairs and helpers on both small and large populations to test whether fragmentation-dispersal or foraging insufficiency was most associated with woodpecker group size. Group pairs were compared with *t*-tests.

RESULTS

As measures of forest fragmentation and habitat loss increased, woodpecker group size in small populations decreased. The number of cuts within 400 m (NCUT 4), the angular sum of cuts within 800 m (ANGSUM), percentage of nonforest area within 400 m (PERCUT4), and 800 m (PERCUT8), were significantly higher in habitat around Red-cockaded Woodpecker clusters that had small group sizes than around large groups (Table 1). Small woodpecker groups were not significantly more isolated (ISOL2KM) than large groups in the small populations (Table 1). The

TABLE 1

COMPARISONS OF SMALL (≤TWO WOODPECKERS, N = 49) AND LARGE (>TWO WOODPECKERS, N = 19) RED-COCKADED WOODPECKER GROUPS ON THREE NATIONAL FORESTS IN EASTERN TEXAS USING MEASURES OF FOREST FRAGMENTATION WITH A *T*-TEST ON DATA FROM SMALL, SPARSE POPULATIONS

Variable	Code	Small group mean (SE)	Large group mean (SE)	*t*	Two-tailed *P*
No. cuts within 400 m	NCUT4	2.1 (0.20)	1.3 (0.3)	2.02	0.047
No. cuts within 800 m	NCUT8	7.0 (0.5)	5.5 (0.9)	1.45	0.153 ns[a]
Angular sum of cuts within 800 m	ANGSUM	226.0 (13.7)	156.8 (25.7)	2.55	0.013
Percentage of nonforest area within 400 m	PERCUT4	24.8 (2.5)	13.3 (4.5)	2.36	0.021
Percentage of nonforest area within 800 m	PERCUT8	26.9 (2.4)	16.2 (4.1)	2.33	0.023
No. active clusters within 2 km	ISOL2KM	2.6 (0.3)	2.3 (0.6)	0.67	0.507 ns[a]

[a] Not statistically significant.

number of woodpeckers per group (NRCWS) decreased significantly as the amount of fragmentation and habitat loss within 400 m and 800 m of active clusters increased (Table 2). Logistic regression indicated that woodpecker group size was a function of the angular sum of forest cuts less than 20 years old in small woodpecker populations ($\chi^2 = 4.73$, $P = 0.030$).

An average of 11.9 ± 10.4 (SD) ha of forest had been removed from the 50-ha area within 400 m of woodpecker clusters and 53.1 ± 37.1 (SD) ha from the 201-ha area within 800 m of woodpecker clusters in our small population study areas (N = 68). In the Angelina National Forest, private inholdings accounted for less than 12% of land area within 400 m of active woodpecker clusters; however, about 49% of forest removal within 400 m of active clusters had occurred on private lands.

A logistic regression comparing active (N = 79) and inactive (N = 90) clusters indicated that cluster status (active vs inactive) was a function of the percentage of nonforest habitat (<20 years old) within 800 m of clusters ($\chi^2 = 4.02$, $P = 0.045$) in small populations. Analyses with small populations and the dense, large population combined indicated that isolation (ISOL2KM, $t = 3.14$, df = 304, $P = 0.002$) and percentage of forest removal within 800 m (PERCUT8, $t = 2.39$, df = 304, $P = 0.017$) were significantly higher around inactive clusters than active clusters.

TABLE 2

CORRELATIONS (r_s) OF MEASURES OF FOREST FRAGMENTATION WITH RED-COCKADED WOODPECKER GROUP SIZE

Variables[a]	NCUT4	NCUT8	ANGSUM	PERCUT4	PERCUT8	ISOL2KM
NRCWS[b]	−0.24	−0.12	−0.28	−0.30	−0.24	0.03
P	0.025	0.157	0.010	0.007	0.026	0.400

[a] See Table 1 for codes.
[b] NRCWS—numbers of woodpeckers per family group (1–5), N = 68.

A comparison of forest habitat loss variables between small and large woodpecker groups in the densely populated portion of the Raven Ranger District revealed that only the number of cuts within 800 m of active clusters (NCUT8) was significantly greater around small family groups (Table 3). Similarly, only NCUT8 was significantly correlated to the number of woodpeckers per group (NRCWS, $r_s = -0.20$, $P = 0.033$).

There were major significant differences between all measures of habitat loss and cluster isolation around dense populations in the Raven Ranger District and the sparse populations in the rest of the National Forest study areas (Table 4). Surprisingly, cutting was significantly more extensive around active clusters from the dense population than around clusters from sparse populations. There were nearly twice as many active clusters within 2 km of each active cluster in the dense population when compared to the sparse populations (Table 4).

In small, sparse populations, comparisons between clusters with only breeding pairs and clusters with breeding pairs and helpers revealed that

TABLE 3

COMPARISON OF SMALL (≤TWO WOODPECKERS, N = 46) AND LARGE (>TWO WOODPECKERS, N = 35) RED-COCKADED WOODPECKER GROUPS IN A DENSE POPULATION IN A PORTION OF THE RAVEN DISTRICT OF THE SAM HOUSTON NATIONAL FOREST

Variable code[a]	Small groups mean (SE)	Large groups mean (SE)	*t*	Two-tailed *P*
NCUT4	3.3 (0.2)	2.7 (0.2)	1.90	0.06 ns
NCUT8	11.2 (0.5)	9.5 (0.4)	2.39	0.01
ANGSUM	285.8 (10.4)	288.3 (9.3)	0.17	0.86 ns
PERCUT4	36.9 (2.9)	36.7 (3.2)	0.04	0.97 ns
PERCUT8	38.4 (2.4)	39.7 (2.8)	0.34	0.73 ns
ISOL2KM	5.0 (0.4)	4.2 (0.5)	1.14	0.25 ns

[a] See Table 1 for codes.

TABLE 4

COMPARISONS OF FOREST FRAGMENTATION AND HABITAT LOSS VARIABLES BETWEEN ACTIVE CLUSTERS IN SMALL, LOW DENSITY RED-COCKADED WOODPECKER POPULATIONS (N = 68) IN THE ANGELINA, DAVY CROCKETT AND EASTERN PORTION OF THE SAM HOUSTON NATIONAL FORESTS AND A LARGER, RELATIVELY HIGH DENSITY POPULATION (N = 81) IN A PORTION OF THE RAVEN RANGER DISTRICT OF THE SAM HOUSTON NATIONAL FOREST

Variable code[a]	Sparse population mean (SE)	Dense population mean (SE)	*t*	Two-tailed *P*
NCUT4	1.9 (0.2)	3.0 (0.2)	5.14	<0.001
NCUT8	6.5 (0.5)	10.4 (0.4)	6.53	<0.001
ANGSUM	206.7 (12.7)	286.9 (7.1)	5.51	<0.001
PERCUT4	21.6 (2.3)	36.8 (2.2)	4.86	<0.001
PERCUT8	24.0 (2.1)	38.9 (1.8)	5.38	<0.001
ISOL2KM	2.5 (0.2)	4.7 (0.3)	5.47	<0.001

[a] See Table 1 for codes.

habitat within 400 and 800 m of pairs with helpers had significantly less forest removal (Table 5). Although habitat around breeding pairs was not significantly different from habitat around single male clusters, means for percentage forest removal and angular sum of cuts were greater for single male clusters. Single male clusters were significantly more isolated than clusters with only breeding pairs (Table 5). There was no significant difference in the isolation of clusters with only breeding pairs and clusters with breeding pairs and helpers.

In the large population in the Raven Ranger District, habitat loss around clusters with only a breeding pair was not significantly different from habitat loss around clusters with breeding pairs and helpers (ANGSUM, $t = 0.16$, $P = 0.87$; PERCUT4, $t = 0.18$, $P = 0.85$; PERCUT8, $t = 0.19$, $P = 0.84$).

Fragmentation appears to have affected a woodpecker group's access to foraging habitat by forcing access routes to go through the territories of adjacent woodpecker groups (Fig. 2). Woodpeckers from cluster 5 in Fig. 2 were forced to forage in the territories of clans from clusters 3, 4, and 6 as a result of cutting that occurred 3–5 years ago. Cluster 5 became inactive during the fall or early winter 1989. All active clusters in Figure 2 have adequate foraging habitat (>51 ha, and >6350 pine stems >26 cm DBH within 800 m) as outlined in the recovery plan (USFWS 1985) and the U.S. Forest Service Red-cockaded Woodpecker management guidelines (USFS 1985). Cluster 2 has 70.3 ha of foraging habitat, cluster 3 has 65.4 ha, and clusters 4, 5, and 6 each have 54.4 ha of nonoverlapping foraging habitat. Woodpeckers from clusters 4 and 6 now frequently forage

TABLE 5

PAIRWISE *T*-TEST COMPARISONS OF THREE RED-COCKADED WOODPECKER GROUP SIZES (SINGLE MALE [SM], BREEDING PAIR [BP], AND BREEDING PAIR PLUS HELPERS [BPH]) WITH MEASURES OF FOREST FRAGMENTATION AND HABITAT LOSS IN THREE NATIONAL FORESTS IN EASTERN TEXAS USING DATA FROM SMALL SPARSE POPULATIONS[a]

Variable	Code	SM mean (SE) N = 15	*t*	*P*	BP mean (SE) N = 34	*t*	*P*	BPH mean (SE) N = 19
No. cuts within 400 m	NCUT4	2.3 (0.4)	0.68	0.50	2.0 (0.2)	1.70	0.09	1.3 (0.3)
No. cuts within 800 m	NCUT8	4.9 (0.8)	0.06	0.95	4.9 (0.5)	0.93	0.35	4.2 (0.6)
Angular sum of cuts within 800 m	ANGSUM	237.8 (26.8)	0.54	0.59	220.9 (16.0)	2.11	0.04	156.8 (25.7)
Percentage of non-forest area within 400 m	PERCUT4	26.8 (4.7)	0.52	0.60	23.9 (3.0)	1.98	0.05	13.3 (4.5)
Percentage of non-forest area within 800 m	PERCUT8	27.1 (5.1)	0.05	0.96	26.9 (2.6)	2.17	0.03	16.2 (4.1)
No. active clusters within 2 km	ISOL2KM	1.8 (0.3)	2.47	0.01	2.9 (0.3)	1.22	0.23	2.3 (0.5)

[a] Group sizes (SM vs BP and BP vs BPH) were compared using two-tailed *t*-test.

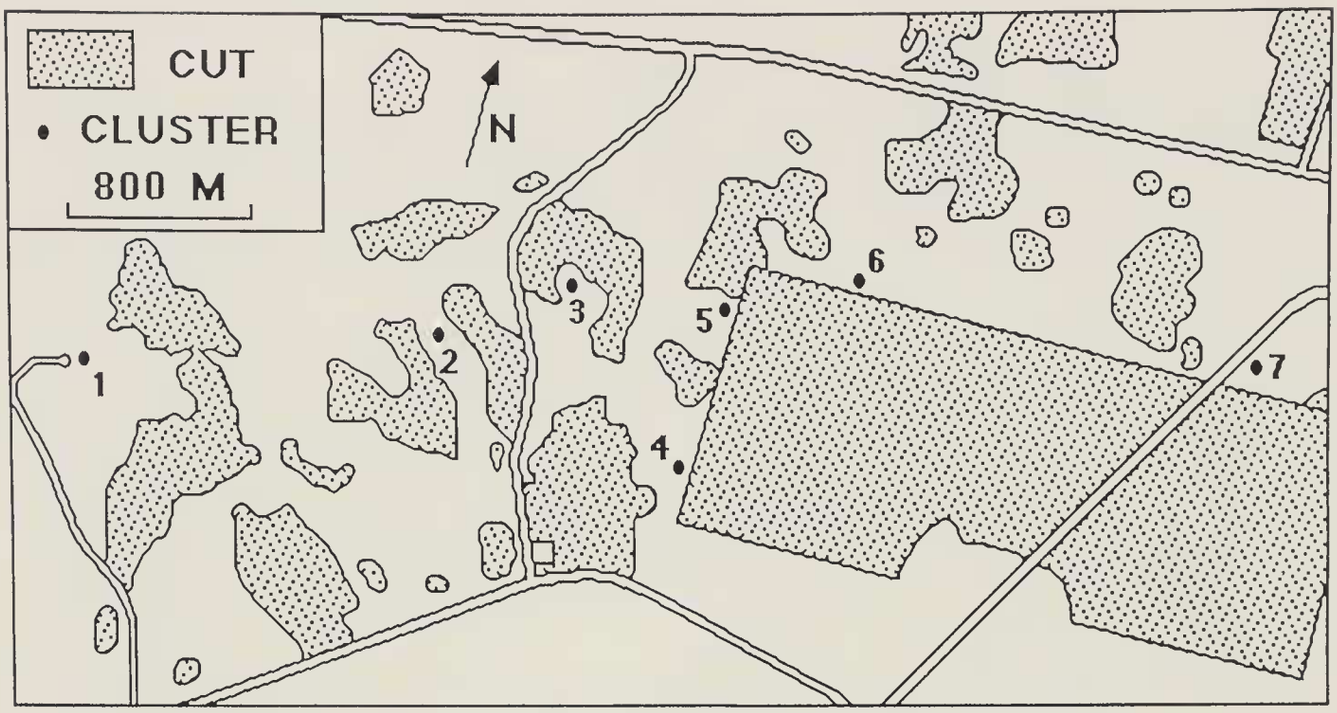

FIG. 2. An example of habitat fragmentation (Federal and private lands) around active Red-cockaded Woodpecker clusters in a National Forest in eastern Texas. Cluster 5 recently became inactive most likely as a result of fragmentation forcing the family group to forage in the territories of groups 3, 4, and 6.

near or within the vacated area of cluster 5. The loss of cluster 5, while surrounded by three active clusters, suggests that foraging habitat was insufficient.

DISCUSSION

Woodpecker group size and cluster status were significantly associated with forest removal for small, sparse Red-cockaded Woodpecker populations. As the amount of forest removal increased, woodpecker group size and the number of active clusters decreased. Isolation and forest removal within 800 m of clusters were significantly associated with cluster inactivation in both large and small populations combined. Our measures of forest loss had little or no relationship with group size in our dense population study area, which suggests that small populations are more vulnerable to forest removal than larger, dense populations. Data presented by Wood et al. (1985) contrast with our observations. In the Wood et al. (1985) study up to 37% of the annual territory of Red-cockaded Woodpecker groups was clearcut without any negative effect on the numbers of nestlings or their survival in the nesting period immediately following clearcutting. The population studied by Wood et al. may have been somewhat larger than the small populations in our study. In our study, group size was not affected by our measures of habitat loss in large populations but was affected in small populations. These results would

be expected if habitat loss is affecting dispersal. If habitat loss affected foraging sufficiency, an effect on group size should appear in both small and large populations; it did not.

If an insufficiency of foraging habitat were the cause of small group size, habitat around clusters with only breeding pairs might be expected to have significantly more forest loss than habitat around clusters with larger groups. Forest loss was greater around clusters with only breeding pairs supporting the hypothesis that habitat loss caused an insufficiency of foraging habitat. However, a portion of the relationship could still be related to the effect of forest fragmentation on female dispersal. Our angular sum measurement, which is more a measure of fragmentation than habitat loss, was greater around clusters with only breeding pairs than clusters with larger family groups.

Habitat loss causing fragmentation could affect breeding frequency if it interferes with the ability of unmated females to find an active group that has lost its breeding female. Fragmentation may reduce the contact between groups necessary for young females to take advantage rapidly of such openings. Any delay in the replacement of a mate would decrease group size in the long run, because no young would be produced during the years when a breeding female was absent. This would decrease the number of male helpers in the long-term because helper males that dispersed or died would not be replaced. We have noticed delays of two to three years for single male clusters to obtain a breeding female in the ANF. A lag period would occur between the time forest removal occurred and a reduction in woodpecker group size was observed. Breeding pairs may live four to five years or longer before one of the pair dies. If the breeding female dies, or the breeding male dies and is replaced by a male offspring, the cluster must be found by a dispersing female (see Walters et al. 1988). Our test of this fragmentation-dispersal hypothesis using a comparison of single male clusters with breeding pair clusters suggests that dispersal was not a problem. Although habitat around clusters with single males had greater habitat loss than clusters with only breeding pairs, the differences were not significant (Table 5).

Most forest removal that has occurred in the areas where our small populations exist (ANF, DCNF, and eastern portion of the SHNF) has occurred within the past four to 20 years. These areas also have extensive and numerous patches of private (non federal) holdings within the outside boundaries of the National Forests that are largely agricultural or other nonforest areas. In contrast, the portion of the Raven Ranger District where the large, dense population exists has few private holdings within it. Also, most loss of forest habitat in the Raven Ranger District occurred around active clusters 3–5 years prior to our study as a result of a major

southern pine beetle (*Dendroctonus frontalis*) epidemic from 1983 to 1985 (Billings and Varner 1986). Although the Raven population has twice as many active clusters around each active cluster than the small populations, it also has had about 15% more forest habitat loss than the small populations (Table 4). If too short a time period has passed to detect an effect of habitat loss on the dense Red-cockaded Woodpecker population in the Raven Ranger District, our results suggest that there may be a major reduction in group size in this population over the next 10 years.

It may be possible to have sufficient foraging habitat within 800 m of an active cluster, and still have insufficient foraging habitat for a woodpecker group because of forest fragmentation. Fragmentation that affects a woodpecker group's access to foraging habitat by forcing access routes to go through the territories of adjacent woodpecker groups may increase the probability of cluster inactivation.

Habitat loss appears to affect woodpecker group size by causing both dispersal and foraging sufficiency problems. It remains difficult to distinguish which mechanism has the greater effect.

ACKNOWLEDGMENTS

We thank S. Loeb and J. Walters for comments on an early draft of the manuscript.

LITERATURE CITED

Billings, R. F. and F. E. Varner. 1986. Why control southern pine beetle infestations in wilderness areas? The four notch and Huntsville State Park experience. Pp. 129–134 *in* Wilderness and natural areas in the eastern United States: a management challenge (D. L. Kulhavy and R. N. Conner, eds.). Center for Applied Studies, School of Forestry, Stephen F. Austin State Univ., Nacogdoches, Texas.

Conner, R. N. and D. C. Rudolph. 1989. Red-cockaded Woodpecker colony status and trends on the Angelina, Davy Crockett, and Sabine National Forests. U.S.D.A. For. Serv., Res. Pap. SO-250.

———, A. E. Snow, and K. A. O'Halloran. 1991. Red-cockaded Woodpecker use of seed-tree/shelterwood cuts in eastern Texas. Wildl. Soc. Bull. 19:67–73.

Diamond, J. M. 1973. Distributional ecology of New Guinea birds. Science 179:759–769.

———. 1976. Island biogeography and conservation: strategy and limitation. Science 193: 1027–1029.

——— and R. M. May. 1976. Island biogeography and the design of nature reserves. Pp. 163–186 *in* Theoretical ecology (R. M. May, ed.). Saunders Company, Philadelphia, Pennsylvania.

Dixon, W. J., M. B. Brown, L. Engelman, J. W. Frame, M. A. Hill, R. I. Jennrich, and J. D. Toporek (eds.). 1985. BMDP statistical software. Univ. of California Press, Berkeley, California.

Doak, D. 1989. Spotted Owls and old growth logging in the Pacific Northwest. Cons. Biol. 3:389–396.

Forsman, E. D., E. C. Meslow, and H. M. Wight. 1984. Distribution and biology of the Spotted Owl in Oregon. Wildl. Monogr. 87.

Galli, A. E., C. F. Leck, and R. T. T. Forman. 1976. Avian distribution patterns in forest islands of different sizes in central New Jersey. Auk 93:356–364.

Harris, L. D. 1984. The fragmented forest. Univ. of Chicago Press, Chicago, Illinois.

Lande, R. 1988. Demographic models of the Northern Spotted Owl (*Strix occidentalis caurina*). Oecologia 75:601–607.

Ligon, J. D., P. B. Stacey, R. N. Conner, C. E. Bock, and C. S. Adkisson. 1986. Report of the American Ornithologists' Union Committee for the conservation of the Red-cockaded Woodpecker. Auk 103:848–855.

MacArthur, R. H. and E. O. Wilson. 1967. The theory of island biogeography. Monogr. Pop. Biol. #1. Princeton Univ. Press, Princeton, New Jersey.

Patterson, G. A. and W. B. Robertson, Jr. 1981. Distribution and habitat of the Red-cockaded Woodpecker in Big Cypress National Preserve. South Florida Research Center Report T-613.

Preston, F. W. 1962a. The canonical distribution of commonness and rarity: part 1. Ecology 43:185–215.

———. 1962b. The canonical distribution of commonness and rarity: part II. Ecology 43: 410–432.

Robbins, C. S., D. K. Dawson, and B. A. Dowell. 1989. Habitat area requirements of breeding forest birds of the middle Atlantic states. Wildl. Monogr. 103.

Rosenberg, K. V. and M. G. Raphael. 1986. Effects of forest fragmentation on vertebrates in Douglas-fir forests. Pp. 263–273 *in* Wildlife 2000, modeling habitat relationships of terrestrial vertebrates (J. Verner, M. L. Morrison, and C. J. Ralph, eds.). Univ. of Wisconsin Press, Madison, Wisconsin.

Simberloff, D. R. 1988. The contribution of population and community biology to conservation science. Ann. Rev. Ecol. Sys. 19:473–511.

SPSSX. 1986. SPSSX. 2nd ed. McGraw-Hill Book Company, New York, New York.

U.S. Fish and Wildlife Service. 1985. Red-cockaded Woodpecker recovery plan. U.S. Fish and Wildlife Service, Atlanta, Georgia.

U.S. Forest Service. 1985. Wildlife habitat management handbook, southern region. Ch. 400—Management by wildlife species: 420—Red-cockaded Woodpecker. USDA For. Serv. FSH-2609.23R, Atlanta, Georgia.

Walters, J. R., P. D. Doerr, and J. H. Carter III. 1988. The cooperative breeding system of the Red-cockaded Woodpecker. Ethology 78:275–305.

Wilcove, D. S. 1989. Forest fragmentation as a wildlife management issue in the eastern United States. Pp. 146–150 *in* Healthy forests, healthy world. Soc. of Am. For., Bethesda, Maryland.

Wilcox, B. A. 1980. Insular ecology and conservation. Pp. 95–117 *in* Conservation biology: an evolutionary-ecological perspective (M. E. Soulé and B. A. Wilcox, eds.). Sinauer Associates, Inc., Sunderland, Massachusetts.

Wood, G. W., L. J. Niles, R. M. Hendrick, J. R. Davis, and T. L. Grimes. 1985. Compatibility of even-aged timber management and Red-cockaded Woodpecker conservation. Wildl. Soc. Bull. 13:5–17.